Morphology, development, and reproduction of *Eyprepocnemis plorans ibandana* (Orthoptera: Acrididae) in South Cameroon rainforests

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Abstract

Eyprepocnemis plorans ibandana is a very common grasshopper species in open environments and agricultural systems of tropical Africa. It is a pest that significantly benefits from forest degradation in southern Cameroon, hence the need to study the bioecology of this subspecies. We studied the reproduction as well as the morphological characteristics and development times of the post-embryonic instars of *E. p. ibandana*. Sixty-one adult pairs were obtained from sixth instar nymphs caught in grassy vegetation in the Nkolbisson area (Yaoundé) and bred in the laboratory. After hatching, the first instar nymphs were individually placed in cages and fed every two days using fresh leaves of *Manihot esculenta*. The postembryonic development of *E. p. ibandana* took six instars in the male and six to seven instars in the female. Mean nymphal development took 79.16 ± 0.51 days in males, 89.93 ± 0.58 days in 6 instar females and 94.96 ± 1.22 days in 7 instar females. The survival rate of the first instar was low (53%). However, from the second instar on the survival rate was very high (> 87%). Sexual dimorphism is distinct in adults, fifth and sixth nymphal instars. Adults of *E. p. ibandana* took on average 32.57 ± 3.88 days to start mating, and mating lasted 2.12 h on average (1–3 h). Oviposition took place on average 52.03 ± 5 days after first mating; each female deposited one to eleven oothecae with an average of 34.93 ± 2.37 eggs per ootheca. Our study provides important information for the control of this subspecies in southern Cameroon.

Keywords

Cameroon, ecology, grasshopper pests, nymphal development

Introduction

Knowledge of an organism's life cycle is a prerequisite for any management, control, or conservation action (see Peveling 2001, Zeug et al. 2012). This is particularly the case for locusts and grasshoppers, some of which are endangered species (Samways et al. 1995, Samways 1997, Samways and Lockwood 1998), while other species are important pests (FAO 2010, 2018, Zhang et al. 2019). For the most important pest species, their life cycle is well known (see Lecoq 1978, Duranton et al. 1982, Gangwere et al. 1997), but some remain largely unstudied despite their economic importance. This is the case for *Eyprepocnemis plorans* (Charpentier, 1825), which has been the subject of only rare studies (Jago 1963, Lecoq 1980, Hernández and Presa 1984, Olmo-Vidal 1990, Schmidt et al. 1996).

Eyprepocnemis plorans — also called Clover or Berseem grasshopper — is widely distributed in Africa, southern Europe, and southwestern Asia, and consists of four geographic subspecies (Jago 1963, Dirsh 1965, Hernández and Presa 1984, Olmo-Vidal 1990, Schmidt et al. 1996, Cigliano et al. 2018). These include *E. p. plorans* (Charpentier, 1825), which occurs in the Mediterranean and western Asia, *E. p. ornatipes* (Walker, 1870), which is found in the Sahelian zone to northern Kenya and southern Arabia, *E. p. meridionalis* (Uvarov, 1921), which is distributed in east and southeastern Africa and *E. p. ibandana* Giglio-Tos, 1907, which occurs in west and central Africa (Dirsh 1965). The latter subspecies is found in forest and pre-forest areas and has been reported from Benin, Côte d'Ivoire, Ghana, Guinea, Liberia, Mali, Nigeria, Togo, South Sudan, Congo, Angola, Uganda, and Cameroon (Mestre and Chiffaud 2006). *E. plorans* is usually regarded as a minor pest, but damage can occasionally be significant, and this species is regarded as an important polyphagous agricultural pest in some countries. This is the case in Egypt, especially in oases and along the Nile (Nakhla 1957, 1976, COPR 1982). In eastern Algeria, this species consumes potatoes, beans, beets, radishes, and spinach (Harrat and Moussi 2007). It is also present on farmland of southern Cameroon (Mestre and Chiffaud 2006), where it damages crops such as cassava, potato, and beans.

Descamps (1953) studied some aspects of the biology of the species in the Sahelian zone of Cameroon, where the subspecies *E. p. ornatipes* is present (Dirsh 1958). Lecoq (1980) studied the life cycle of *E. p. ornatipes* in the Sudanese zone of West Africa and identified two generations per year and a period of quiescence at the imaginal stage during the dry season. In forest regions where *E. p. ibandana* occurs, the life cycle of the species has not yet been

investigated. This is unfortunate not only because of the species' increasing ravaging activities facilitated by forest degradation in southern Cameroon, but also because of data on the life cycles of different subspecies across various eco-geographical regions in the world (Jago 1963, Lecoq 1980, Hernández and Presa 1984, Olmo-Vidal 1990, Schmidt et al. 1996).

In the Sahelian zone, this species is found throughout the year as both nymphs and adults (Lecoq 1988). In Spain, there is only one generation per year, from July to March (Hernández and Presa 1984). Schmidt et al. (1996) bred up to four generations per year in the laboratory of *E. p. plorans* from Sardinia. They observed six post-embryonic nymphal instars in the male and seven instars in the female (mean development time 25 ± 9 days) without any diapause. In *E. p. meridionalis* from Tanzania, Jago (1963) found seven instars in the male and seven to eight in the female. However, data on the life cycle, reproductive biology, and nymphal development of *E. p. ibandana* are lacking. This study aimed to collect these data; specifically, we aimed (1) to determine the number and duration of nymphal instars of *E. p. ibandana*, (2) to morphologically describe each instar, (3) to study the survival rates of these different instars, and (4) to study the reproductive behavior of *E. p. ibandana* in southern Cameroon.

Methods

Study area.—The individuals raised in the laboratory were caught between August 2014 and March 2017 at Nkolbisson, Yaoundé. Yaoundé is located in a semi-deciduous forest area, but the natural vegetation is highly degraded because of anthropic activity. The region is characterized by alternating hills and swamps (Bachelier 1959). The climate is of Guinean equatorial type with four seasons: a short rainy season (mid-March to June), a short dry season (July and August), a long rainy season (September to mid-November), and a short dry season (from mid-November to mid-March). The rainfall is about 1,600 mm per year and temperature varies from 19° to 33°C (Suchel 1987).

Sampling.—Adults of *E. p. ibandana* (n = 61 adult pairs) used in this study were obtained from sixth instar nymphs collected on grass vegetation at Nkolbisson using a sweep net. Nymphs were transported to the laboratory in cylindrical polypropylene plastic boxes (type 1 cages: 9 cm high and 13 cm in diameter) closed with a wire mesh lid. In the laboratory, these nymphs were reared individually in the same type 1 cages on a shelf.

Meteorological data collection in the laboratory.—Temperature and relative humidity (RH) in the laboratory were recorded daily during the experiment (morning, afternoon, and evening) with a Gottingen Thermohygrograph. The temperature and RH during the breeding period are provided in Fig. 1.

Reproduction.—After the final molt of the specimens collected in the field, the adults were paired in 15 wire cages (type 2 cages: 11 cm high and 10 cm in diameter) closed by a mesh cover. Each cage was one third filled with heat-sterilized wet sand, serving as an oviposition medium. Observations were conducted every two days to record pre-mating, mating, oviposition, and hatching dates.

Post-embryonic development.—First instar nymphs obtained from each adult pair were counted and placed individually in type 1 cages, then kept on shelves for development monitoring. A dry stem of *Chromolaena odorata* (14 cm long) was placed in each cage

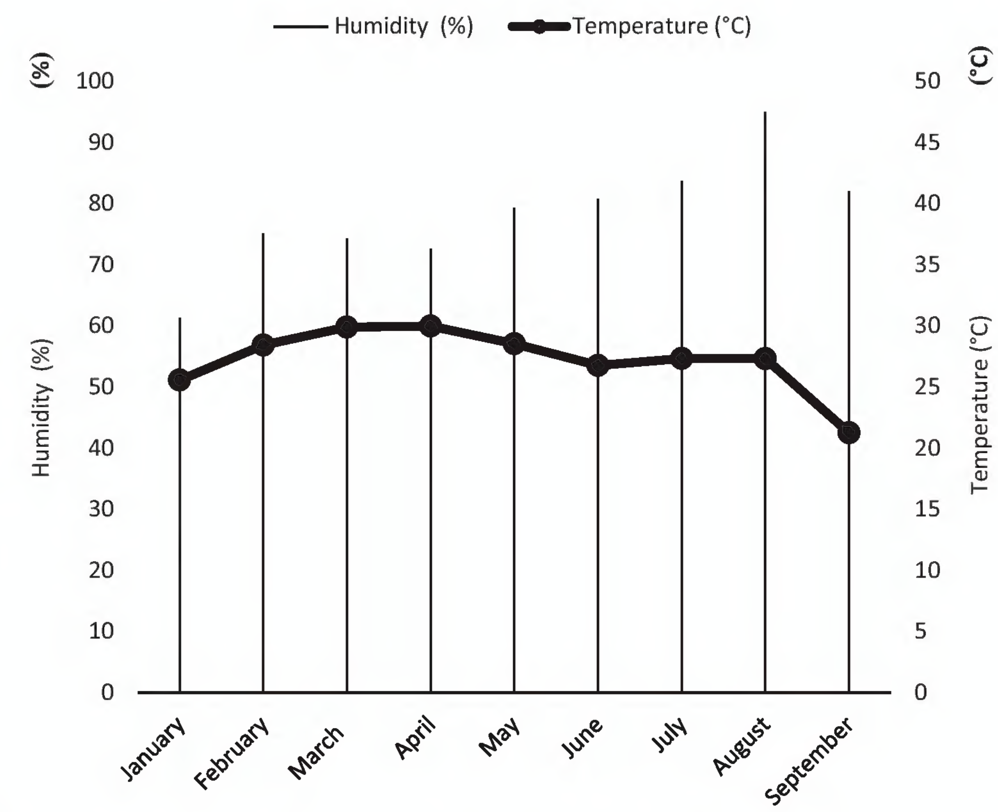

Fig. 1. Variation in temperature and relative humidity from January to September 2017. Laboratory of Zoology Faculty of Science University of Yaoundé 1.

to support molting of the nymphs. Each cage was labeled with hatching date, number, stage, and sex. Each nymph was fed every two days with a cassava leaf (*Manihot esculenta*). The presence of exuviae was recorded daily and the state (dead or alive) of the nymphs was noted. The cages were also cleaned and the leaves used as food were renewed.

Morphology and morphometrics.—The morphology and morphometry of *E. p. ibandana* were recorded from freshly dead individuals during rearing. The morphological characteristics were observed using a Heerbrugg binocular lens. For each developmental instar, measurements were made and, for paired structures, the right structure was measured and their shape and color were described. The following parameters were measured as described by De Grégorio (1987) and Default (2012): Total body length (Lt): from the tip of the fastigium to the tip of the abdomen, measured in lateral view; length of cephalic capsule (Lcc): length of head from the tip of the fastigium to the most posterior part of the head, measured in dorsal view; width of cephalic capsule (lcc): head width including compound eyes, measured in dorsal view; length of thorax (Lth): from the anterior to posterior margin of pronotum; length of abdomen (Labd): from posterior margin of pronotum to tip of abdomen, measured in lateral view; length of pronotum (Lpr): along midline, measured in dorsal view; length of antenna (La): from the scape to the apex of the last segment of flagellum; number of antennal articles (Na) in the flagellum; length of tegmina (Lel): from the insertion point to the apex of tegmen, measured in dorsal view; length of hind wing (Lai): from the insertion point to the apex of wing, measured in dorsal view; length of hind femur (Lcu1): maximum length of hind femur; length of median femur (Lcu2): maximum length of median femur; length of anterior femur (Lcu3): maximum length of anterior femur; length of hind tibia (Lti1): maximum length of hind tibia; length of mid tibia (Lti2): maximum length of mid tibia; length of anterior tibia (Lti3): maximum length of anterior tibia; number of external spines on hind tibia (Nse).

Drawings were made with the same magnifying glass in a light chamber and at 25–50X magnification.

Data analysis.—Data were analyzed using Excel (version 2016) and PAST (version 2.5) softwares. Excel was used to draw the different curves; PAST was used to calculate averages of development times and morphometric parameters. The averages were compared with the Kruskal-Wallis and Mann Whitney tests at the 5% significance level.

Results

Number of instars and duration of postembryonic development.—In the laboratory, nymphal development of *E. p. ibandana* went through six instars in males and six (75% of females) to seven (25% of females) instars in females (Table 1). The average total development time differed significantly ($p < 0.0001$) between the sexes: 79.16 ± 0.51 (54 to 124 days) in the males, 89.93 ± 0.58 (67 to 131 days) in six-instar females, and 94.96 ± 1.22 (67 to 161 days) in seven-instar females (Table 1). From the fifth nymphal instar onwards, average development times differed significantly ($p<0.0001$) from one instar to another (Table 1).

Nymphal survival rate.—We obtained 2,603 hatchlings, 793 (30.46%) of which reached the adult stage. The transition from the first instar (L1) to the second (L2) was marked by a very high mortality rate (47%), but from the L2 instar on the survival rate was high, with values between 87% and 92% (Fig. 2), resulting in a linear decreasing number of individuals from L2 to the adult stage (Fig. 2).

Reproduction: courtship, mating, and oviposition.—Courtship began 32.47 ± 3.88 days (8 to 59 days) after the final molt, by contact of the palps and antennae between both sexes. The male clung to her pronotum; when the latter was not receptive, the male remained on her back (this could last more than 2 hours). In some cases, the female used her hind legs to prevent the male from clinging to her. When the female was receptive, the male clung to her pronotum with his prothoracic and mesothoracic legs, the metathoracic legs being free and folded. In this position, the male bent his abdomen about 180° to the left or right below that of the female in order to bring the two genital regions into contact. He then introduced his phallus between the genital valves of the female to the vaginal opening. The coupling ($n = 61$) lasted for 2.12 h on average (between 1 and 3 hours) if uninterrupted.

After pairing, the first ootheca was deposited 9 to 70 days later (average 52.03 ± 5 days). Females laid between 1 to 11 egg pods (average 3 ± 1.4) and the number of eggs per ootheca ranged from 14 to 50 (34.93 ± 2.37 on average). On average, the females took 52.02 ± 5.1 days for laying of the first pod, 73.23 ± 6.84 days for the second pod, and 101.3 ± 10.31 days for the third pod.

Morphology of the different developmental stages.—

Egg: The eggs of *E. p. ibandana* are 3 to 5.5 mm long (average 4.37 ± 0.44 mm) and 1 to 1.5 mm in diameter (average 1.00 ± 0.05 mm). The eggs have a yellowish color, an elongated shape, are slightly curved and with rounded ends.

Adults: The general body color is of a variable brown, sometimes light beige, or brown-gray. The eyes are streaked with a small black band highlighting the sub-ocular suture. The pronotal disc is flat, with weakly pronounced lateral carina that are blurred in the metazona; the posterior border is slightly angular. The pronotal disc has two light bands running along the lateral carina and surrounding a dark brown zone; the dark zone narrows towards the anterior and posterior margins; the prosternal process is cylindrical. The elytra and wings are fully developed, slightly shorter, reaching or extending beyond the posterior apex of the abdomen and bearing a beige longitudinal stripe in the median field. The lower outer half of the posterior femora is usually yellow or light beige, lighter than the upper half. The basal half of the posterior tibiae is blue, the apical half reddish with whitish spines and black apices. The posterior tarsi are red.

Males are 21 to 27 mm long (average 24.33 ± 1.60 mm). The head is between 5 and 7 mm (average 6.30 ± 0.67 mm) long; the

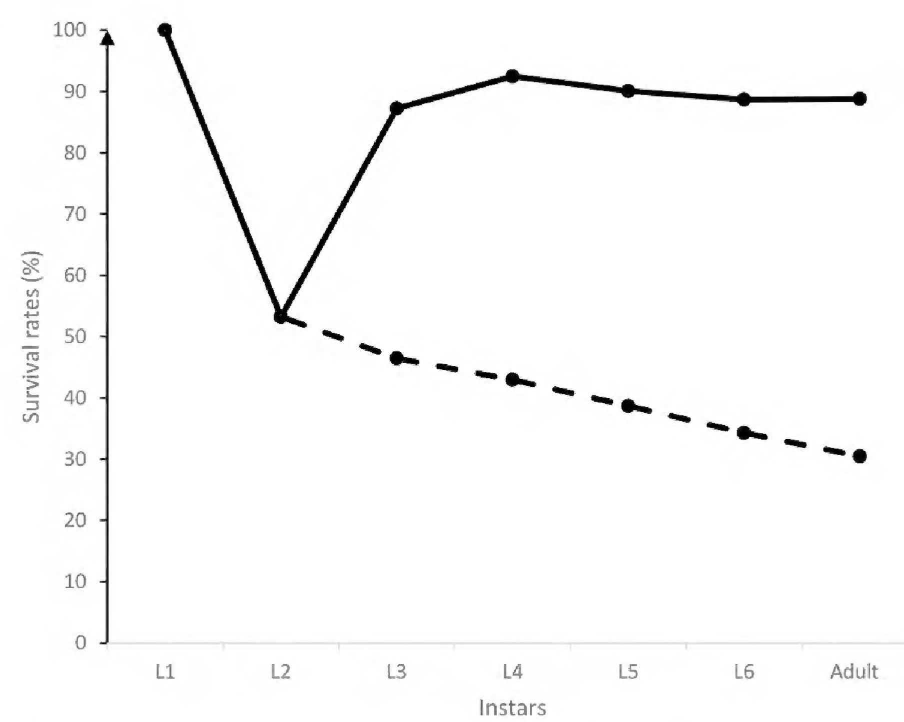

Fig. 2. Survival rate of the nymphal instars of *E. p. ibandana* in the laboratory. Solid line: % survival of each instar; broken line: % of all nymphs still surviving. L1–L6 = nymphal instars 1–6.

Table 1. *Eyprepocnemis plorans ibandana*, male and female nymphal instars average development time (mean ± standard error in days), under laboratory conditions. Number of specimens: 388 males, 325 six instar females, 143 seven instar females.

Sexes	Instars							Kruskal Wallis Test		Total duration
	L1 Nymph	L2 Nymph	L3 Nymph	L4 Nymph	L5 Nymph	L6 Nymph	L7 Nymph	H Value	P Value	
Males										
Duration	12.22±0.13^{aA}	11.32±0.17^{bAB}	11.53±0.17^{bAB}	12.64±0.19^{aA}	13.5±0.20^{cA}	18±0.28^{dA}	–	517	<0.0001	79.16±0.51^{A}
Range	(4–28)	(4–24)	(2–33)	(6–38)	(6–46)	(6–38)				(54–124)
Females of six instars										
Duration	12.78±0.17^{aB}	11.70±0.19^{bA}	12.10±0.22^{bA}	13.72±0.25^{cB}	14.92±0.31^{dB}	24.72±0.48^{eB}	–	249.4	<0.0001	89.93±0.58^{B}
Range	(6–26)	(4–28)	(4–27)	(4–33)	(2–48)	(9–51)				(67–131)
Females of seven instars										
Duration	12±0.27^{aAB}	10.81±0.24^{bB}	11.19±0.30^{bB}	12.74±0.40^{aA}	13±0.34^{aC}	14.27±0.42^{cC}	20.52±0.63^{d}	260.9	<0.0001	94.96±1.22^{C}
Range	(6–26)	(2–21)	(2–27)	(4–33)	(5–32)	(4–37)	(5–56)			(67–161)

Notes: Values in table indicate: mean ± standard error (Min–Max). Legend: Uppercase letters compare values vertically; lowercase letters compare values horizontally.

Fig. 3. *Eyprepocnemis plorans ibandana*, male from Ongot, Cameroon.

Fig. 4. *Eyprepocnemis plorans ibandana*, female, from Ongot, Cameroon.

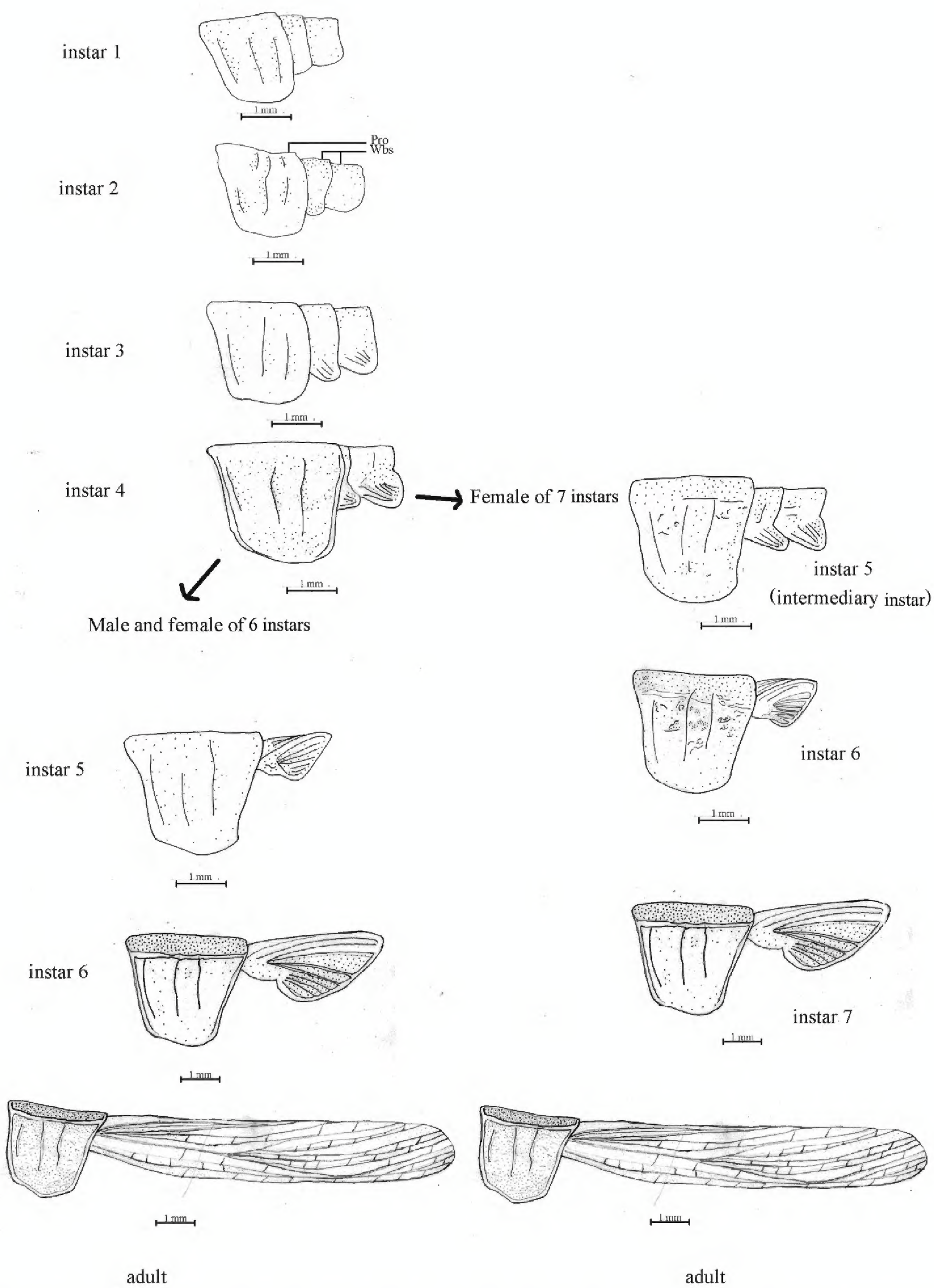

Fig. 5. *Eyprepocnemis plorans ibandana*, postembryonic development of pronotum and wings (lateral view). Pro: pronotum; Wbs: Wing buds.

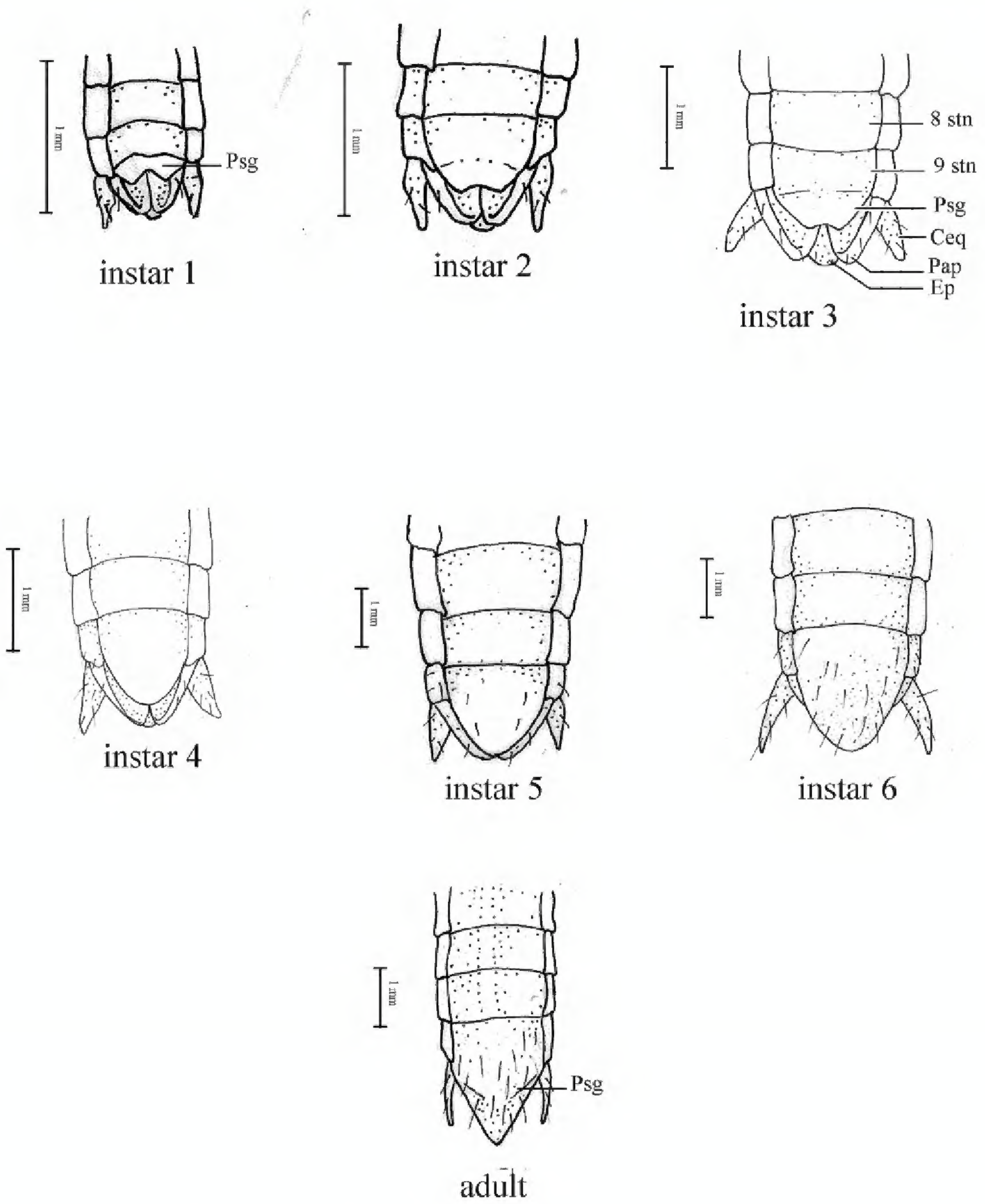

Fig. 6. *Eyprepocnemis plorans ibandana*, postembryonic development of males' external genitalia (ventral view). Ceq: cerci, Ep: epiproct, Pap: paraproct, Psg: subgenital plate, 8 stn: sternite 8, 9 stn: sternite 9.

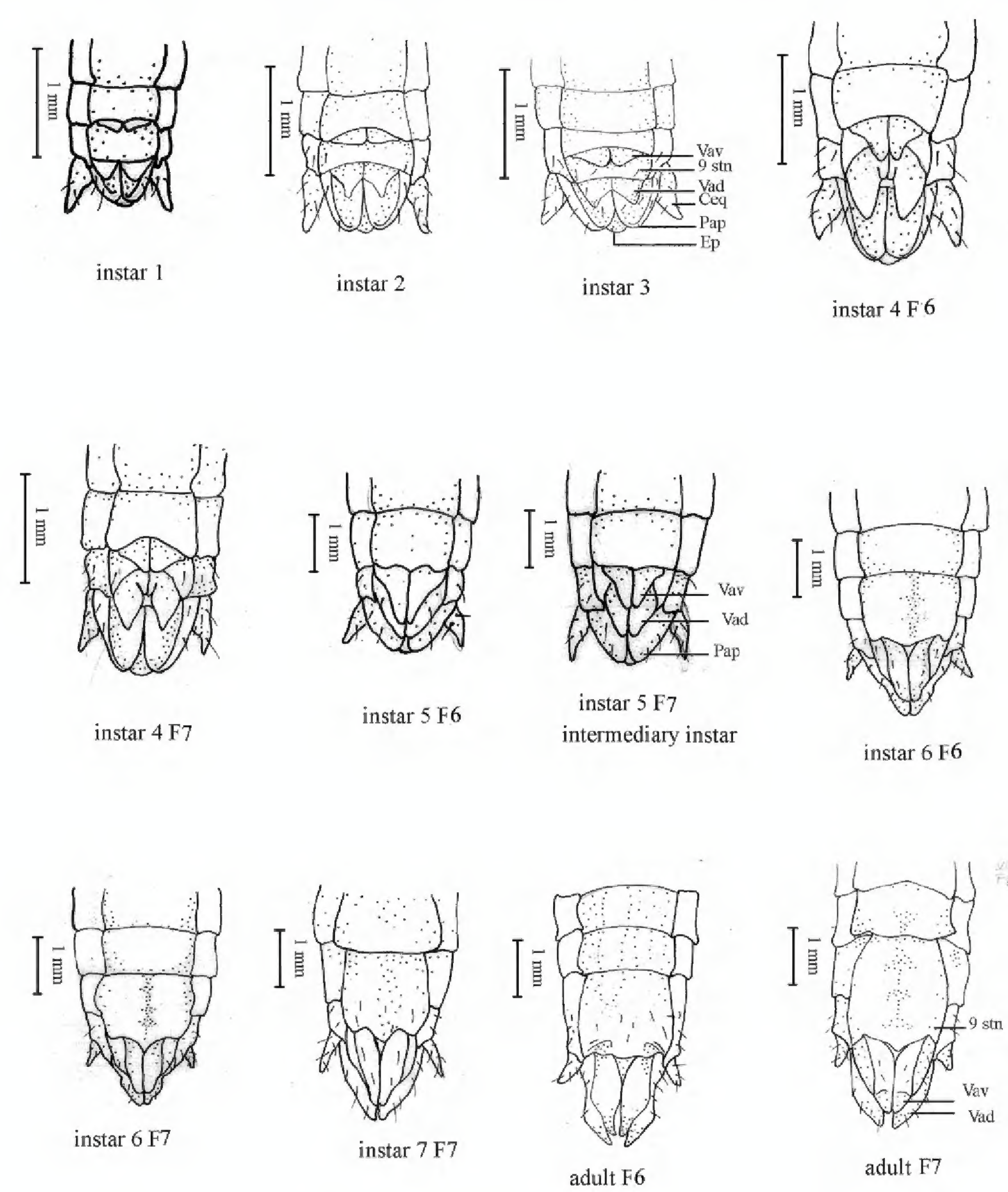

Fig. 7. *Eyprepocnemis plorans ibandana*, postembryonic development of females' external genitalia (ventral view). Ceq: cerci, Ep: epiproct, Pap: paraproct, Vad: dorsal valve, Vav: ventral valve, 9 stn: sternite 9, F6: female of six instars, F7: female of seven instars.

eyes bear six longitudinal eye stripes; the antenna carries 24 articles, measures 9.90 to 10 mm (average 9.99 ± 0.03 mm) and reaches dorsally almost the posterior margin of the pronotum. The thorax measures 6 to 9 mm (average 7.72 ± 0.98 mm); the pronotal disc measures between 4 and 5 mm (average 4.81 ± 0.37 mm). The abdomen is 11 to 14 mm long (average 12.74 ± 0.84 mm); the sub-genital plate is conical with acute apex (Figs 3, 5, 6 and Table 2).

Females that passed through six nymphal instars have a body of 29.80 to 41.70 mm (average 35.86 ± 2.94 mm) long. The head measures 7.10 to 10 mm (average 8.45 ± 0.65 mm); the antenna carries 24 to 25 articles, measures between 9.30 and 12 mm (average 10.74 ± 0.73 mm), and reaches dorsally almost the posterior margin of the pronotum. The eyes bear six clearly visible longitudinal eye stripes. The thorax measures between 9 and 12 mm (average 10.44 ± 0.77 mm). The pronotal disc is between 5.50 and 7 mm (average 6.35 ± 0.49 mm) long. The abdomen measures between 17 and 27.50 mm (average 21.79 ± 2.7 mm). The genital valves are very robust and slightly curved towards the rear. The posterior margin of sternite 8 is undulating without a median process (Figs 4, 5, 7 and Table 2).

Females that passed through seven nymphal instars are not significantly different in size than females that have passed through six instars (Table 2), but they are distinctive in having an eye with seven clearly visible longitudinal eye stripes; the pronotal disc has in its middle part a clearly visible median dark band, surrounded by two clearly visible pale beige lateral carinae and the posterior margin of sternite 8 carries a small median process (Figs 5, 7, and Table 2).

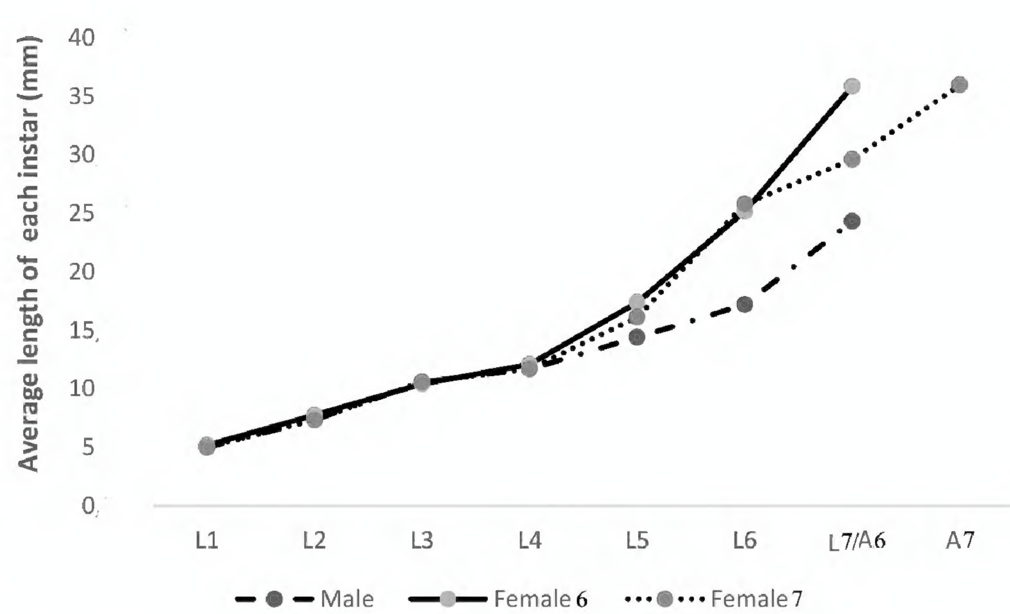

Fig. 8. *Eyprepocnemis plorans ibandana*, increase in body size under laboratory conditions. L= nymph; A= adult.

Common characteristics of the nymphal instars.—The body is usually dark brown in color with spots and light beige bands. The head is weakly conical, dark brown in color with a beige band behind each compound eye, extending onto the anterior border of the pronotum. The fastigium is trapezoid in shape with a slight mid and concave longitudinal depression; it is brown, with a midlength pale beige band extending over the pronotum to the posterior end of the abdomen. The face is light beige with brown spots; the frontal ridge is concave with two more or less parallel longitudinal carinae reaching the base of the mouthparts. The pronotum is cylindrical in shape, weakly roof-like, bearing three brown sutures

Table 2. *Eyprepocnemis plorans ibandana*, male and female measurements of morphological characters.

Instars	Sex/type	Lt	Lcc	lcc	Lth	Labd	Lpr	La	Na
L1	Male	5.01±0.63 (3.20–6.00) (32) A	2.01±0.14 (1.30–2.20) (32) A	1.26±0.12 (1.00–1.50) (32) A	1.83±0.26 (1.20–2.50) (32) A	2.12±0.29 (1.40–2.60) (32) A	0.98±0.06 (0.80–1.10) (32) A	1.70±0.23 (1.10–2.10) (32) A	11±00 (11–11) (32) A
	Female	5.19±0.78 (3.80–6.90) (30) A	2.10±0.17 (2.00–2.90) (30) A	1.29±0.16 (1.00–1.50 (30) A	1.73±0.34 (1.00–2.10) (30) A	2.49±0.60 (1.70–3.90) (30) A	0.98±0.04 (0.90–1.00) (30) A	1.77±0.16 (1.40–2.10) (30) AB	10.63±0.49 (10–11) (30) A
L2	Male	7.35±0.83 (5.90–8.80) (30) B	2.31±0.18 (2.10–2.90) (30) AB	1.83±0.13 (1.50–2.00) (30) B	2.29±0.28 (1.90–3.00) (30) B	3.96±0.56 (2.50–5.00) (30) B	1.29±0.12 (1.10–1.70) (30) B	2.16±0.13 (1.90–2.50) (30) B	15±00 (15–15) (30) B
	Female	7.76±0.73 (6.50–9.30) (30) B	2.48±0.28 (1.30–2.80) (30) B	1.94±0.08 (1.80–2.00) (30) B	2.45±0.25 (2.00–3.00) (30) B	4.05±0.47 (3.00–5.00) (30) B	1.39±0.12 (1.20–1.60) (30) B	2.28±0.18 (2.00–2.60) (30) B	15±00 (15–15) (30) B
L3	Male	10.58±0.76 (9.00–12.00) (30) C	3.18±0.15 (2.90–3.50) (30) C	2.17±0.09 (2.00–2.30) (30) BC	3.29±0.26 (2.80–4.00) (30) C	5.76±0.52 (5.00–7.00) (30) C	1.94±0.08 (1.80–2.00) (30) C	3.07±0.09 (2.90–3.30) (30) C	16.87±0.34 (16–17) (30) C
	Female	10.46±0.72 (9.00–11.50) (28) C	3.21±0.16 (3.00–3.50) (28) C	2.19±0.07 (2.10–2.30) (28) C	3.34±0.28 (2.80–3.80) (28) C	5.69±0.52 (4.60–6.40) (28) C	1.97±0.05 (1.80–2.00) (28) C	3.05±0.12 (2.80–3.30) (28) C	16.71±0.46 (16–17) (28) C
L4	Male	11.71±1.76 (10.1–14.00) (30) C	3.77±0.29 (3.30–4.60) (30) D	2.79±0.34 (2.40–3.90) (30) D	3.60±0.39 (3.00–4.50) (30) C	6.30±0.88 (5.20–8.00) (30) C	2.35±0.24 (2.00–3.10) (30) D	3.78±0.30 (3.20–4.50) (30) D	19.06±0.36 (18–20) (30) D
	Female	12.10±1.38 (9.40–15.00) (31) C	3.85±0.37 (3.00–4.90) (31) D	2.75±0.28 (2.00–3.20) (31) D	3.73±0.46 (2.80–4.70) (31) CD	6.47±0.74 (5.00–8.10) (31) C	2.41±0.34 (1.90–3.00) (31) D	3.84±0.47 (2.90–5.00) (31) D	19.03±0.18 (19–20) (30) D
L5	Male	14.40±1.56 (12.1–18.00) (33) D	4.40±0.27 (4.00–5.00) (33) E	3.09±0.11 (3.00–3.30) (33) E	4.09±0.41 (3.50–5.00) (33) DE	8.04±1.34 (6.10–11.00) (33) D	3.16±0.09 (3.00–3.30) (33) E	4.91±0.27 (4.20–5.30) (33) E	21.09±0.68 (20–22) (33) E
	Female 6	17.3±0.95 (16.00–18.3) (23) E	5.50±0.41 (4.90–6.00) (23) F	3.87±0.21 (3.50–4.00) (23) F	4.93±0.26 (4.30–5.10) (23) F	9.81±0.60 (9.20–10.60) (23) E	4.04±0.16 (3.70–4.20) (23) F	6.09±0.65 (5.00–7.40) (23) F	21.00±00 (21–21) (23) E
	Female 7	16.05±1.65 (14.5–18.00) (20) E	4.58±0.45 (4.10–5.10) (20) E	3.30±0.26 (3.00–3.60) (20) E	4.26±0.84 (3.30–5.10) (20) E	9.44±1.07 (8.40–10.70) (20) E	3.12±0.15 (3.00–3.30) (20) E	4.64±0.30 (4.30–5.00) (20) E	21.00±00 (21–21) (20) E
L6	Male	17.20±1.36 (15.0–19.2) (36) E	5.01±0.16 (4.80–5.50) (36) G	3.62±0.28 (3.20–4.00) (36) G	5.27±0.39 (4.80–6.00) (36) F	9.44±1.19 (7.50–11.00) (36) E	3.96±0.23 (3.50–4.30) (36) F	6.23±0.42 (5.50–7.00) (36) F	23.00±00 (23–23) (36) F
	Female 6	25.17±2.00 (21.0–27.0) (30) F	7.18±0.53 (6.50–8.00) (30) H	5.04±0.46 (4.20–5.50) (30) H	7.09±0.57 (6.00–7.70) (30) G	13.88±1.94 (11.0–16.0) (30) F	5.74±0.40 (5.10–6.10) (30) G	8.76±0.95 (7.30–10.00) (30) GH	23.00±00 (23–23) (30) F
	Female 7	25.80±0.54 (25.2–26.7) (32) F	6.93±0.26 (6.50–7.30) (32) H	5.52±0.52 (5.00–6.10) (32) I	7.10±0.25 (6.70–7.50) (32) G	15.15±0.39 (14.8–16.00) (32) G	5.98±0.16 (5.70–6.20) (32) H	8.44±0.88 (7.00–10.00) (32) G	23.00±00 (23–23) (32) F
L7	Female 7	25.61±2.13 (21.0–27.0) (38) F	6.93±0.23 (6.50–7.20) (38) H	4.94±0.31 (4.30–5.30) (38) H	7.15±0.49 (6.10–7.50) (38) G	15.31±1.52 (12.0–16.3) (38) G	5.97±0.22 (5.50–6.20) (38) GH	9.02±0.88 (7.30–10.00) (38) H	24.00±00 (24–24) (38) G
Adult	Male	24.33±1.60 (21.0–27.0) (25) F	6.30±0.67 (5.00–7.00) (25) I	3.99±0.33 (3.90–4.00) (25) F	7.72±0.98 (6.00–9.00) (25) H	12.74±0.84 (11.0–14.0) (25) F	4.81±0.37 (4.00–5.00) (25) I	9.99±0.03 (9.90–10.00) (25) I	24.00±00 (24–24) (25) G
	Female 6	35.86±2.94 (29.8–41.7) (36) G	8.45±0.65 (7.10–10.0) (36) J	5.42±0.36 (5.00–6.00) (36) I	10.44±0.77 (9.00–12.00) (36) I	21.79±2.79 (17.0–27.5) (36) H	6.35±0.49 (5.5–7.0) (36) J	10.74±0.73 (9.30–12.00) (36) J	24.05±0.23 (24–25) (36) G
	Female 7	35.78±4.40 (30.0–44.0) (26) G	8.36±0.42 (8.0–9.20) (26) J	5.43±0.37 (5.00–6.00) (26) I	10.69±1.01 (9.00–13.00) (26) B	23.17±3.94 (17.0–29.00) (26) I	6.36±0.47 (5.7–7.0) (26) J	10.52±0.63 (9.0–11.0) (26) J	24.23±0.43 (24–25) (26) G

Notes: Each value of the table represents: mean and standard error (min- max) (sample size). Within columns, means with same letters are not significantly different. Legend: Lt: length of body. Lcc: length of cephalic capsule. lcc: width of cephalic capsule. Lth: length of thorax. Labd: length of abdomen. Lpr: length of pronotum. La: length of antenna. Na: Number of antennal articles. Lel: length of elytra. Lai: length of the hind wing. Lcu1, Lcu2 and Lcu3: length of femur 1, length of femur 2, length of femur 3. Lti1, Lti2, Lti3: length of tibia 1, length of tibia 2, length of tibia 3. Nse: Number of external spines on hind tibia. L= nymphal instars.

Table 2. Continued. *Eyprepocnemis plorans ibandana*, male and female measurements of morphological characters.

Instars	Sex/type	Lel	Lail	Lcu1	Lcu2	Lcu3	Lti1	Lti2	Lti3	Nse
L1	Male	–	–	0.98±0.04 (0.9–1.00) (32) A	1.06±0.06 (0.90–1.10) (32) A	3.05±0.09 (2.70–3.20) (32) A	0.99±0.03 (0.90–1.00) (32) A	1.09±0.17 (1.00–2.00) (32) A	2.96±0.13 (2.40–3.10) (32) A	1.00±0.00 (1.00–1.00) (32) A
	Female	–	–	0.99±0.04 (0.90–1.10) (30) A	1.08±0.06 (0.90–1.20) (30) A	3.07±0.11 (2.90–3.30) (30) A	0.98±0.04 (0.90–1.00) (30) A	1.06±0.06 (0.90–1.20) (30) A	2.94±0.10 (2.70–3.00) (30) A	1.00±0.00 (1.00–1.00) (30) A
L2	Male	–	–	1.12±0.06 (1.00–1.30) (30) A	1.26±0.09 (1.10–1.50) (30) AB	4.04±0.18 (3.60–4.30) (30) B	1.13±0.06 (1.00–1.30) (30) AB	1.30±0.10 (1.10–1.50) (30) B	3.75±0.19 (3.10–3.90) (30) B	2.00±0.00 (2.00–2.00) (30) B
	Female	–	–	1.17±0.09 (1.00–1.40) (30) A	1.36±0.16 (1.10–1.70) (30) B	4.31±0.25 (3.60–4.80) (30) B	1.15±0.08 (1.00–1.30) (30) B	1.35±0.12 (1.20–1.60) (30) B	3.92±0.22 (3.40–4.30) (30) B	2.00±0.00 (2.00–2.00) (30) B
L3	Male	–	–	1.69±0.08 (1.60–1.90) (30) B	1.85±0.16 (1.20–2.00) (30) C	5.64±0.32 (5.10–6.10) (30) C	1.63±0.14 (1.40–1.90) (30) C	1.85±0.13 (1.50–2.00) (30) C	4.70±0.30 (4.10–5.80) (30) C	3.00±0.00 (3.00–3.00) (30) C
	Female	–	–	1.70±0.11 (1.50–2.00) (28) B	1.91±0.09 (1.70–2.00) (28) C	5.71±0.22 (5.40–6.20) (28) C	1.61±0.11 (1.40–1.90) (28) C	1.90±0.10 (1.70–2.00) (28) C	4.77±0.17 (4.30–5.20) (28) C	3.00±0.00 (3.00–3.00) (28) C
L4	Male	–	–	2.02±0.15 (1.80–2.50) (30) C	2.17±0.26 (1.90–3.00) (30) CD	7.24±0.66 (6.20–9.00) (30) E	2.01±0.21 (1.80–2.50) (30) D	2.27±0.24 (2.00–2.90) (30) D	5.87±0.44 (5.10–7.10) (30) D	4.00±0.00 (4.00–4.00) (30) D
	Female	–	–	2.04±0.19 (1.70–2.70) (31) C	2.16±0.28 (1.60–3.10) (31) D	7.33±0.86 (5.40–9.20) (31) E	1.96±0.18 (1.60–2.30) (31) D	2.35±0.29 (2.00–3.00) (31) D	6.07±0.57 (4.70–7.50) (31) D	4.00±0.00 (4.00–4.00) (31) D
L5	Male	2.11±0.13 (1.90–2.30) (33) A	2.32±0.22 (2.10–2.70) (33) A	2.52±0.36 (1.90–3.00) (33) D	2.85±0.18 (2.50–3.00) (33) E	9.31±0.75 (8.30–11.10) (33) F	2.49±0.24 (2.20–2.90) (33) E	3.13±0.29 (3.00–4.00) (33) E	7.49±0.40 (6.70–8.00) (33) E	5.00±0.00 (5.00–5.00) (33) E
	Female 6	2.82±0.27 (2.30–3.00) (23) A	3.04±0.22 (2.50–3.20) (23) A	3.08±0.17 (2.80–3.30) (23) E	3.51±0.32 (3.00–3.90) (23) F	12.14±0.77 (10.90–12.9) (23) G	3.03±0.23 (2.70–3.50) (23) F	3.97±0.23 (3.40–4.20) (23) F	9.58±0.58 (8.80–10.10) (23) F	5.00±0.00 (5.00–5.00) (23) E
	Female 7	1.25±0.19 (1.20–1.30) (20) A	1.19±0.10 (1.10–1.30) (20) B	2.61±0.26 (2.20–2.90) (20) D	2.86±0.24 (2.60–3.10) (20) E	9.50±0.64 (8.50–10.20) (20) F	2.51±0.24 (2.00–2.70) (20) E	3.05±0.27 (2.50–3.30) (20) E	7.61±0.58 (7.00–8.30) (20) E	5.00±0.00 (5.00–5.00) (20) E
L6	Male	5.55±0.68 (4.00–7.00) (36) B	4.90±0.48 (4.10–6.00) (36) C	3.13±0.19 (3.00–3.70) (36) E	3.67±0.31 (3.10–4.00) (36) F	11.58±0.76 (10.3–13.1) (36) G	3.10±0.24 (2.90–4.00) (36) F	3.88±0.20 (3.50–4.20) (36) F	8.93±0.59 (8.00–10.00) (36) G	6.00±0.00 (6.00–6.00) (36) F
	Female 6	8.01±1.64 (5.20–9.50) (30) C	9.44±1.07 (8.40–10.70) (30) D	4.23±0.60 (3.20–4.80) (30) F	4.69±0.46 (4.00–5.10) (30) G	16.63±0.99 (15.0–18.0) (30) H	4.12±0.10 (4.00–4.10) (30) GH	5.15±0.08 (5.00–5.20) (30) GH	13.14±0.88 (11.5–14.00) (30) H	6.00±0.00 (6.00–6.00) (30) F
	Female 7	8.10±0.18 (7.90–8.40) (32) C	7.09±0.58 (6.10–8.00) (32) D	4.57±0.14 (4.30–4.70) (32) F	5.16±0.19 (5.00–5.50) (32) H	16.87±0.90 (15.2–18.00) (32) H	4.18±0.14 (4.00–4.40) (32) G	5.23±0.20 (5.00–5.50) (32) G	13.19±0.81 (12.0–14.0) (32) I	6.00±0.00 (6.00–6.00) (32) F
L7	Female 7	8.10±0.77 (7.00–10.80) (38) C	7.15±0.51 (6.20–8.00) (38) D	4.44±0.34 (4.00–5.00) (38) F	4.90±0.40 (4.00–5.20) (38) GH	16.83±1.06 (15.0–18.0) (38) H	4.12±0.08 (4.00–4.20) (38) GH	5.15±0.11 (5.00–5.30) (38) GH	12.36±0.45 (11.6–13.20) (38) J	7.00±0.00 (7.00–7.00) (38) G
Adult	Male	20.22±1.57 (17.0–23.0) (25) D	18.29±1.62 (15.3–21.0) (25) E	4.92±0.39 (4.00–5.70) (25) G	5.59±0.39 (5.00–6.00) (25) I	14.66±0.91 (13.0–16.0) (25) I	3.98±0.28 (3.00–4.90) (25) H	4.98±0.22 (4.50–5.90) (25) H	12.31±0.61 (11.0–13.0) (25) J	6.00±0.00 (6.00–6.00) (25) F
	Female 6	28.35±2.05 (23.5–32.00) (36) E	26.07±2.23 (21.5–30.0) (36) F	5.45±0.41 (5.00–6.00) (36) H	6.34±0.44 (5.50–7.00) (36) I	20.83±0.39 (17.0–26.5) (36) J	5.01±0.18 (4.60–5.50) (36) I	6.75±0.45 (6.00–7.30) (36) I	16.39±0.89 (15.0–18.1) (36) K	6.00±0.00 (6.00–6.00) (36) F
	Female 7	28.06±2.63 (24.0–32.0) (26) E	25.61±2.74 (21.5–30.0) (26) F	5.48±0.37 (5.00–6.00) (26) H	6.36±0.44 (6.00–7.10) (26)	20.88±1.82 (17.0–23.2) (26) J	5.23±0.33 (4.90–6.00) (26) J	6.56±0.33 (4.90–6.00) (26) I	16.75±1.11 (14.9–18.6) (26) K	7.00±7.00 (7.00–7.00) (36) S

Notes: Each value of the table represents: mean and standard error (min- max) (sample size). Within columns, means with same letters are not significantly different. Legend: Lt: length of body. Lcc: length of cephalic capsule. lcc: width of cephalic capsule. Lth: length of thorax. Labd: length of abdomen. Lpr: length of pronotum. La: length of antenna. Na: Number of antennal articles. Lel: length of elytra. Lai: length of the hind wing. Lcu1, Lcu2 and Lcu3: length of femur 1, length of femur 2, length of femur 3. Lti1, Lti2, Lti3: length of tibia 1, length of tibia 2, length of tibia 3. Nse: Number of external spines on hind tibia. L= nymphal instars.

dotted with beige spots forming the median carina. The mesosternal space is open, much wider than long, with rounded lobes. The elytra are absent. The abdomen has ten segments visible dorsally and nine visible ventrally. The cerci are conical with an acute apex slightly exceeding the epiproct. The epiproct is triangular, bifurcated and with a rounded apex dorsally beyond the paraprocts (Figs 5–7 and Table 2).

Identification key for post-embryonic instars.—Refer to the key of Jago (1963) on *Eyprepocnemis plorans meridionalis*.

Sexual dimorphism.—We observed a clear sexual dimorphism from 5th nymphal instar to adults. At these instars, the length of body, head, thorax, abdomen, pronotum, antennae, elytra, wings, femora, and metathoracic tibiae are larger in females than in males.

Growth rate.—The growth rate was similar for both sexes from the first nymphal instar to the fourth. Starting from 5th instar, the growth of males became slower than that of the two types of females (six and seven instar females). At the sixth nymphal instar, six instars females increased faster in size than seven instar females, but as the latter passed through an additional instar, there was no significant difference between the sizes of the two types of adult females (Fig. 8).

Discussion

Postembryonic development of E. p. ibandana.—Our study showed that the number of instars varies between the two sexes in *E. p. ibandana*: six in the male and six or seven in the female, confirming the results obtained by Jago (1963) for *E. p. meridionalis*, Hernández and Presa (1984) in Spain for *E. p. plorans*, and Schmidt et al. (1996) in Sardinia. In southern Cameroon, the nymphal development of three pyrgromorphid grasshoppers (*Zonocerus variegatus*, *Pyrgomorpha vignaudii*, *Taphronota ferruginae*) has been studied previously (Kekeunou 2007, Kekeunou et al. 2015, Kekeunou et al. 2018), all of which had a fixed number of six instars in both sexes. On the other hand, a variable number of instars is well known for many Orthoptera species (Uvarov 1966).

The tropical grasshopper *Cornops aquaticum* may have five to seven nymphal instars depending on the host plant, humidity, and its distribution range from Mexico to Argentina (Adis and Wolfgang 2003, Adis et al. 2004). This could be explained by the genetic and environmental indices that are known to be factors affecting growth rates and number of nymphal instars in Orthoptera (Hochkirch and Gröning 2008). This means that females can maximize their fitness by reaching a larger adult body size, which allows them to produce more eggs, while males can maximize their lifetime reproductive success through multiple mating for a relatively short period of time (Sai-Keung 1973, Shine 1989, Hochkirch and Gröning 2008). This is due to the differences in activity patterns of the molting glands, corpora allata, and corpora cardiaca between the sexes. Indeed, molt and metamorphosis in hexapods depend on the circulating peak of ecdysone and juvenile hormone in both sexes (Joly 1968).

From our results, the nymphal development of *E. p. ibandana* was longer than in Jago's (1963) study on *E. p. meridionalis*, which obtained for the male and the female 55.3 and 59.45 days, respectively. These differences may be explained by the different rearing conditions of both studies. Jago (1963) reared his material in the laboratory (approximately 25°C) in UK, while our study was done in Cameroon in semi-outdoor rearing conditions subject to natural variations in temperature. Differences in temperature are an important reason for the differences observed: our work better reflected field conditions and our results may be closer to what happens in nature than in the laboratory study of Jago (1963). The duration of development is strongly influenced by temperature in all insects (Ratte 1984) as well as by the host plants, e.g., Halouane (1997) and Ould El Hadj et al. (2004) found, respectively, 41 and 43.58 days for nymph development of *S. gregaria* on cabbage, while Ghidaoui (1990) and Ouchene (1995) found, respectively, 61.22 and 29.6 days on lemon and cabbage plus grass. An additional factor influencing development is the size of the cages. Kaufmann (1965) has shown that the life cycle of *Z. variegatus* is shorter in large cages than in smaller cages.

Nymphal survival rate.—The survival rate of the first nymphal instar was quite low in our study compared to the later instars. This lower survival of first instars in the laboratory and in nature is common in other grasshoppers and locusts, e.g., desert locust, Australian plague locust (Dhouib 1994, Seddik 1994, Symmons and Cressman 2001, Ould El Hadj et al. 2004). This reflects a high sensitivity of first nymphal instar that is related to variations in environmental conditions and possibly the monospecific diet they were subjected to in the laboratory. Indeed, *E. p. ibandana* is a species of mesophilic environments with a polyphagous diet in the field (Blanchet 2009). According to Kekeunou et al. (2018), the high mortality of young nymphs could be explained by problems such as inadequate watering, molting, and nutrition. In our study the nymphs were fed with leaves of a single food plant; the nature of this monospecific diet may have affected nymphal development.

Reproduction of E. p. ibandana.—The mating of *E. p. ibandana* is similar to that observed in most other short-horned grasshoppers (Duranton and Lecoq 1990, Symmons and Cressman 2001, Dushimirimana et al. 2012), including also some species from Cameroon such as *T. ferruginea* (Kekeunou et al. 2018), *P. vignaudii* (Kekeunou et al. 2015), and *Z. variegatus* (Kekeunou 2007). Mating started on average 32.47 days after the final molt. This result differs from those obtained by Kekeunou et al. (2018) on *T. ferruginea* and Kekeunou et al. (2015) on *P. vignaudii*, who assessed the time between fledging and first mating at 42.47 days and 12.7 days, respectively. These differences could be explained not only by the time required for each species to reach sexual maturity, but also by the time needed to find favorable ecological conditions, adequate temperature and humidity, and availability of food (Duranton and Lecoq 1990).

We found that a female of *E. p. ibandana* lays between one and eleven oothecae during her adult life-span. The number of eggs per egg pod ranged from 14 to 50. In the laboratory, *S. gregaria* females produce a mean of 22 pods, each containing 47.6 eggs (Wang and Sehnal 2002), which suggests that they produce a total of 1,050 eggs during their entire reproductive life (Dushimirimana et al. 2012). For the same species, Norris (1952) reports 5–9 pods (each pod contained 10 to 140 eggs), while Popov (1958) found no more than 2 or 3 egg-pods for each female. In nature, Chapman et al. (1986) observed 17–77 eggs per ootheca in *Z. variegatus*, but only 6.5 eggs on average by *Miramella alpina* feeding on *Vaccinium myrtillus* and *V. uliginosum* (Asshoff and Hättenschwiler 2005). These differences could be explained by the fact that the number of eggs per ootheca depends on the environmental conditions in which the insects live (Joly 1968), as well as the number of ovarioles of each ovary (Chiffaud and Mestre 1990). Whitman (2008) and Ackman and Whitman (2008) have also shown that a

number of other factors, such as the length of the pre-oviposition period and the number of females participating in reproduction, also influence the reproductive capacity of a population.

Sexual dimorphism in E. p. ibandana.—Sexual dimorphism is marked in adults, as well as in 5th and 6th nymphal instar of *E. p. ibandana*. These results corroborate those of Hochkirch and Gröning (2008) who state that in 99% of Caelifera, adult females are larger than males. The larger size of the females probably reflects the need for egg production (Duranton and Lecoq 1990).

Two major hypotheses have been proposed to explain the ultimate causes of dimensional dimorphism: the intersexual competition hypothesis and the differential equilibrium hypothesis (Hochkirch and Gröning 2008). The first suggests that sexual dimorphism is a mechanism to reduce intra-specific competition, allowing the sexes to specialize in different foods. The differential equilibrium hypothesis proposes that different body sizes represent fitness optima of specific sexual shapes, which are caused by their specific life history strategies. Females can maximize their reproductive success by increasing the number (or size) of eggs (selection of fecundity), while males can maximize their reproduction by being more mobile and fertilizing many females in a short time (Hochkirch and Gröning 2008).

Conclusion

Under laboratory conditions, nymphal development of *E. p. ibandana* fed on cassava went through six instars in males and six (75%) or seven (25%) instars in females. The average development time in days was 79.16 in males and 89.93 to 94.96 in females. Fifth and sixth nymphal instars showed slightly longer development times. The survival rate of the first nymphal instar was low in our study compared to the later instars. Data on instar recognition and development times are useful for treatment programs by providing information on what stage the grasshoppers are at and how much time is left for treatment before the more damaging adult stage. It also gives an idea of how quickly treatments need to be performed to reduce nymphal populations in the field and reduce damage.

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References

Ackman O, Whitman DW (2008) Analysis of body size and fecundity in a grasshopper. Journal of Orthoptera Research 17: 249–257. https://doi.org/10.1665/1082-6467-17.2.249

Adis J, Lhano M, Hill M, Wolfgang JJ, Marques MI, Oberholzer H (2004) What determines the number of juvenile instars in the tropical grasshopper *Cornops aquaticum* (Leptysminae: Acrididae: Orthoptera)? Studies on Neotropical Fauna and Environment 39: 127–132. https://doi.org/10.1080/01650520412331271729

Adis J, Wolfgang JJ (2003) Feeding impact and bionomics of the grasshopper *Cornops aquaticum* on the water hyacinth *Eichhornia crassipes* in central Amazonian floodplains. Studies on Neopropical Fauna and Environment 38: 245–249. https://doi.org/10.1076/snfe.38.3.245.28167

Asshoff R, Hättenschwiler S (2005) Growth and reproduction of the alpine grasshopper *Miramella alpina* feeding on CO_2-enriched dwarf shrubs at treeline. Oecologia 142: 191–201. https://doi.org/10.1007/s00442-004-1714-0

Bachelier G (1959) Etude pédologique des sols de Yaoundé. Contribution à l'étude de la pédogénèse des sols ferrallitiques. Agronomie Tropicale 14: 280–305.

Blanchet E (2009) Développement des marqueurs moléculaires chez les Orthoptères: application à l'étude du genre *Calliptamus*. Thèses de Doctorat, Montpellier, France: Université Montpellier III – Paul Valéry.

Chapman RF, Page WW, McCaffery AR (1986) Bionomics of the variegated grasshopper (*Zonocerus variegatus*) in West & Central Africa. African Journal of Biotechnology 33: 479–505. https://doi.org/10.1146/annurev.en.31.010186.002403

Chiffaud J, Mestre J (1990) Le Criquet puant *Zonocerus variegatus* (Linne, 1758). Essai de synthèse bibliographique. CIRAD-PRIFAS, 140 pp.

Cigliano MM, Braun H, Eades DC, Otte D (2018) Orthoptera Species File. Version 5.0/5.0. http://Orthoptera.SpeciesFile.org

COPR (1982) The Locust and Grasshopper Agricultural Manual. Centre for Overseas Pest Research, London.

De Grégorio R (1987) *Zonocerus variegatus* (Orthoptera, Pyrgomorphidae): caractéristiques morphologiques et biométriques des larves des populations des saisons sèche et humide. Bulletin de la société d'histoire naturelle de Toulouse 123: 29–44.

Default B (2012) Biométrie des types des Caelifères de France (Orthoptera). 1. Définition des paramètres mesurés. 2. Mensurations chez les Tridactylidae, Tetrigidae, Pyrgomorphidae, Pamphagidae et Acrididae Calliptaminae. Matériaux Orthoptériques et Entomocénotiques 17: 21–56.

Descamps M (1953) Observations relatives au criquet migrateur africain et à quelques autres espèces d'Acrididae du Nord Cameroun. Agronomie Tropicale 8: 567–613.

Dhouib S (1994) Action de quelques substrats alimentaires sur la croissance, le développement et la structure de la cuticule chez le criquet pèlerin *Schistocerca gregaria* (Forskål, 1775) (Orthoptera Acrididae). Mémoire d'ingénieur agronome, Ouargla, Algeria: Institut National de Formation Agronomique Saharienne.

Dirsh VM (1958) Synonymic and taxonomic notes on Acrididea (Orthoptera). Revista Española de Entomologia. Eos 34: 25–32.

Dirsh VM (1965) The African Genera of Acridoidea. Anti-locust Research Centre, London, 578 pp.

Duranton JF, Launois M, Launois-Luong MH, Lecoq M (1982) Acridiens (Orthoptères). In: Appert J, Deuse J (Eds) Les ravageurs des cultures vivrières et maraîchères sous les tropiques. Maisonneuve et Larose, Paris, and ACCT, 61–74.

Duranton JF, Lecoq M (1990) Le criquet pèlerin au Sahel. Collection Acridologie Opérationnelle n° 6, Comité Inter-Etats de Lutte contre la Sécheresse dans le Sahel, Département de Formation en Protection des végétaux, Niamey, and CIRAD/PRIFAS, Montpellier, 178 pp.

Dushimirimana S, Hance T, Damiens D (2012) Comparison of reproductive traits of regular and irradiated male desert locust *Schistocerca gregaria* (Orthoptera: Acrididae): Evidence of last-male sperm precedence. Biology Open 1: 232–236. https://doi.org/10.1242/bio.2012323

FAO (2010) Locust watch: Locusts in Caucasus and Central Asia. Food and Agriculture Organization of the United Nations. http://www.fao.org/ag/locusts-CCA/en/index.html

FAO (2018) Locust watch: Desert locust. Updated June 4. Food and Agricultural Organization of the United Nations. http://www.fao.org/ag/locusts/en/info/info/index.html

Gangwere SK, Muralirangan MC, Muralirangan M (1997) The Bionomics of Grasshoppers, Katydids and their Kin. CAB International, Wallingford, UK, 83–101.

Ghidaoui H (1990) Elevage du criquet pèlerin *Schistocerca gregaria* (Forskål, 1775) et impact de divers substrats alimentaires sur la reproduction. Mémoire, ISH, Sousse, Tunisia, 44 pp.

Halouane F (1997) Cycle biologique de *Schistocerca gregaria* (Forskål, 1775) et de *Locusta migratoria* (Linné, 1758) (Orthoptera, Acrididae). Efficacité de *Metarhizium anisopliae* (Meth) (Hyphomycetes, Deuteromycotina) et effet sur quelques paramètres physiologiques de *Schistocerca gregaria*. Mémoire, INA, El Harrach, Algeria, 237 pp.

Harrat A, Moussi A (2007) Inventaire de la faune acridienne dans deux biotopes de l'Est Algérien. Sciences & Technologie 26: 99–105.

Hernández F, Presa JJ (1984) Sobre la biología de *Eyprepocnemis plorans* (Charpentier, 1825) (Orthoptera: Acrididae), en la huerta de Murcia (S.E. España). Boletín de Sanidad Vegetal. Plagas 10: 245–249.

Hochkirch A, Gröning J (2008) Sexual size dimorphism in Orthoptera. Journal of Orthoptera Research 17: 189–196. https://doi.org/10.1665/1082-6467-17.2.189

Jago ND (1963) Some observations on the life cycle of *Eyprepocnemis plorans meridionalis* Uvarov, 1921, with a key for the separation of nymphs at any instar. Proceedings of the Entomological Society of London, 38: 113–124. https://doi.org/10.1111/j.1365-3032.1963.tb00765.x

Joly P (1968) Endocrinologie des Insectes. Masson & Cie, Paris, 344 pp.

Kaufmann T (1965) Observations on the aggregation, migration and feeding habits of *Zonocerus variegatus* in Ghana. Annals of the Entomological Society of America 58: 791–801. https://doi.org/10.1093/aesa/58.4.426

Kekeunou S (2007) Influence des différents types de végétations de jachères sur les populations de *Zonocerus variegatus* (Linné, 1758) (Orthoptera: Pyrgomorphidae) dans la zone de forêt humide du Sud-Cameroun. Thèse de doctorat, Département de Biologie Animale de la Faculté des Sciences de l'Université de Yaoundé 1, Cameroun, 197 pp.

Kekeunou S, Mbeng D, Oumarou Ngoute C, Wandji AC (2015) Morphology, development and reproduction of *Pyrgomorpha vignaudii* (Orthoptera: Pyrgomorphidae). Entomological Research 45: 58–70. https://doi.org/10.1111/1748-5967.12097

Kekeunou S, Wandji AC, Oumarou Ngoute C (2018) Morphology, postembryonic development and reproduction of *Taphronota ferruginea* (Fabricius, 1781) (Orthoptera: Pyrgomorphidae). Tropical Zoology 31: 68–84. https://doi.org/10.1080/03946975.2018.1445686

Lecoq M (1978) Biologie et dynamique d'un peuplement acridien de zone soudanienne en Afrique de l'Ouest (Orthoptera, Acrididae). Annales de la Société Entomologique de France (NS) 14: 606–681.

Lecoq M (1980) Biologie et dynamique d'un peuplement acridien de zone soudanienne en Afrique de l'Ouest (Orthoptera, Acrididae). Note complémentaire. Annales de la Société Entomologique de France (N.S.) 16: 49–73. http://agritrop.cirad.fr/390863

Lecoq M (1988) Les criquets du Sahel. Collection Acridologie Opérationnelle n°1, Comité Inter-Etats de Lutte contre la Sécheresse dans le Sahel, Département de Formation en Protection des végétaux, Niamey, and CIRAD/PRIFAS, Montpellier, 129 pp.

Mestre J, Chiffaud J (2006) Catalogue et atlas des acridiens de l'Afrique de l'Ouest. J. Mestre & J. Chiffaud-Mestre, Groléjac, France, 350 pp.

Nakhla NB (1957) The life-history, habits and control of the bersim grasshopper, *Eyprepocnemis plorans* Charp., in Egypt (Orthoptera: Acrididae). Bulletin de la Societé Entomologique d'Egypte 41: 411–427.

Nakhla NB (1976) The population density of the Berseem grasshopper, *Eyprepocnemis plorans plorans* Charp., as related to environment and control [in Egypt Arab Republic]. Plant Production and Protection Div. Report N° FAO-AGP--DL/TS/16; FAO-AGP--INT/71/030, FAO, Rome.

Norris MJ (1952) Reproduction in the desert locust (*Schistocerca gregaria* Forskål) in relation to density and phase. Anti-Locust Bulletin 13: 1–51.

Olmo-Vidal JM (1990) Atlas of the Orthoptera of Catalonia. Atlas of Biodiversity 1: 337–458.

Ouchene D (1995) Quelques aspects biologiques de *Schistocerca gregaria* (Forskål, 1775) (Orthoptera, Acrididae) dans la région de Tamanrasset et en conditions contrôlées. Mémoire, INA, El Harrach, Algeria, 85 pp.

Ould El Hadj MD, Tankari Dan-Badjo A, Halouane F (2004) Etude du cycle biologique de *Schistocerca gregaria* (Forskål, 1775) sur chou (*Brassica oleracea*) en laboratoire. Université Mohamed Khider, Biskra, Algeria, Courrier du Savoir 5: 17–21.

Peveling R (2001) Environmental conservation and locust control – possible conflicts and solutions. Journal of Orthoptera Research 10: 171–187. https://doi.org/10.1665/1082-6467(2001)010[0171:ECALCP]2.0.CO;2

Popov GB (1958) Note on the frequency and the rate of oviposition in swarms of the Desert Locust (*Schistocerca gregaria* Forskål). Entomologist's Monthly Magazine 94: 176–180.

Ratte HT (1984) Temperature and Insect Development. Environmental Physiology and Biochemistry of Insects. Springer, Heidelberg, Berlin, 304 pp. http://link.spriger.com/content/pdf/10.1007%2F978-3-642-70020-0pdf

Sai-Keung L (1973) The postembryonic development of *Atractomorpha sinensis* Bolivar with particular reference to the phallic structures (Orthoptera: Acridoide: Pyrgomorphidae). Master of Science, McGill University Montreal, 179 pp.

Samways MJ (1997) Conservation biology of Orthoptera. In: Gangwere SK, Muralirangan MC, Muralirangan M (Eds) Bionomics of Grasshoppers, Katydids and their Kin. CAB International, Wallingford, 481–496.

Samways MJ, Lockwood JA (1998) Orthoptera conservation: Pests and paradoxes. Journal of Insect Conservation 2: 143–149. https://doi.org/10.1023/A:1009652016332

Samways MJ, Stork NE, Cracraft J, Eeley HAC, Foster M, Lund G, Hilton-Taylor C (1995) Scales, planning and approaches to inventorying and monitoring. In: Heywood VH, Watson RT (Eds) Global Biodiversity Assessment. United Nations Environment Programme, Cambridge University Press, Cambridge, 517–475.

Schmidt GH, Friedel K, Rembold H (1996) Studies on the size of corpora allata, the juvenile hormone III titre in the haemolymph and growth of terminal oocytes throughout three consecutive gonadotropic cycles in *Eyprepocnemis plorans* (Orthopteroidea: Caelifera: Acrididae). European Journal of Entomology 93: 131–144.

Seddik A (1994) Développement ovarien et charge alaire du criquet pèlerin : *Schistocerca gregaria* (Forskål, 1775) (Orthoptera-Acrididae) et du criquet migrateur : *Locusta migratoria cinerascens* Bonnet et Finot, 1889 (Orthoptera-Acrididae) à Adrar. Cycle biologique du criquet pèlerin au laboratoire. Mémoire, INA, El Harrach, 141 pp.

Shine R (1989) Ecological causes for the evolution of sexual dimorphism: A review of the evidence. Quarterly Review of Biology 64: 419–461. https://doi.org/10.1086/416458

Suchel JB (1987) Les climats du Cameroun. Les climats du Cameroun. Thèse de doctorat d'état, Bordeaux, Université de Bordeaux III, France.

Symmons PM, Cressman K (2001) Desert Locust Guideline. Biology and Behaviour. Food and Agriculture Organization of the United Nations, Rome 25pp.

Uvarov BP (1966) Grasshoppers and Locusts. University Press, Cambridge, 481 pp.

Wang F, Sehnal F (2002) Ecdysteroid agonist RH-2485 injected into *Schistocerca gregaria* (Orthoptera: Acrididae) females accelerates oviposition and enhances ecdysteroid content in eggs. Applied Entomology and Zoology 37: 409–414. https://doi.org/10.1303/aez.2002.409

Whitman DW (2008) The significance of body size in the Orthoptera: A review. Journal of Orthoptera Research 17: 117–134. https://doi.org/10.1665/1082-6467-17.2.117

Zeug SC, Bergman PS, Cavallo BJ, Jones KS (2012) Application of a life cycle simulation model to evaluate impacts of water management and conservation actions on an endangered population of Chinook salmon. Environmental Modeling and Assessment 17: 455–467. https://doi.org/10.1007/s10666-012-9306-6

Zhang L, Lecoq M, Latchininsky A, Hunter D (2019) Locust and grasshopper management. Annual Review of Entomology 64: 15–34. https://doi.org/10.1146/annurev-ento-011118-112500